A simple test of vocal individual recognition in wild meerkats

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ABSTRACT

Individual recognition is thought to be a crucial ability facilitating the evolution of animal societies. Given its central importance, much research has addressed the extent of this capacity across the animal kingdom. Recognition of individuals vocally has received particular attention due, in part, to the insights it provides regarding the cognitive processes that underlie this skill. Whilst much work has focused on vocal individual recognition in primates, there is currently very little data showing comparable skills in non-primate mammals under natural conditions. This may be because non-primate mammal societies do not provide obvious contexts in which vocal individual recognition can be rigorously tested. We addressed this gap in understanding by designing an experimental paradigm to test for individual recognition in meerkats (*Suricata suricatta*) without having to rely on naturally occurring social contexts. Results suggest that when confronted with a physically impossible scenario – the presence of the same conspecific meerkat in two different places – subjects responded more strongly than during the control, physically possible setup. We argue that this provides the first clear evidence for vocal individual recognition in wild non-primate mammals and hope that this novel experimental design will allow more systematic cross-species comparisons of individual recognition under natural settings.

1. INTRODUCTION

Individual recognition of conspecifics is considered to be crucial to the evolution of animal sociality [1, 2]. Given its central importance, much research has addressed the competence of numerous animal species in this behavioural and cognitive domain [3]. Due to their rich and multifaceted social lives, primates have received particular attention, with numerous studies demonstrating individual recognition through the playback of vocalizations [see 4]. Evidence for equivalent abilities in wild non-primates is much less clear for two reasons: (1) it has proven difficult to find socially meaningful contexts where individual vocal identification would be more advantageous than class-level vocal recognition, other than mother-infant interactions [5, 6], and (2) social and ecological differences make it hard to find a good experimental framework for cross-species comparisons [7]. We addressed these issues by devising a novel violation-of-expectation paradigm favouring individual recognition in meerkats (*Suricata suricatta*), but which does not depend on naturally occurring social interactions.

Meerkats, like primates, rely heavily on vocal communication to coordinate their activities according to their surrounding ecological situation, such as the risk of predation [8]. However, exactly how important vocalizations are for tracking changes in their social environment is currently not clear [9]. During social foraging, meerkats frequently emit stereotyped, individually distinctive, 'close calls', which most likely function in maintaining group cohesion [10]. Using a dual-speaker setup we simulated two physical scenarios: 1) incongruent (test) condition: the same subordinate meerkat foraging on one side of the subject and then within a few seconds (physically impossible) appearing on the geometrically opposite side; and 2) congruent (control) condition: two subordinates foraging independently

on either side of the subject. If meerkats use vocalizations to recognize and track conspecific group members individually, we predicted they should respond more during the incongruent, physically impossible condition, in terms of vigilance behaviour and looking in the direction of the expectancy violation (loudspeaker from which the 2nd playback was broadcast), than during the socially and physically congruent condition.

2. METHODS

Study site and subjects

Recordings and playback experiments were conducted on wild but habituated meerkats at the Kalahari Meerkat Project (KMP), South Africa [8], between October-December, 2010 (see ESM).

Call recording and playback construction

We recorded close calls from male subordinate meerkats (>12 months) belonging to the same group as playback subjects at a distance of approximately 1-2m, using a Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-state recorder. In one group subordinate females were recorded and used as playback stimuli, as no males in this group were habituated to a sufficient level to allow good quality call collection. Calls were transferred digitally onto a PC using Cool Edit Pro 2000. Up to six foraging close calls with a high signal-to-noise ratio were selected randomly from sound files and used to construct playbacks. In the test and control conditions two independent playbacks of 4.5secs consisting of between 2-3 close calls were created (see ESM). In the test (incongruent) condition, the two playback files consisted of different close calls recorded from the same individual. In the control (congruent) condition one playback file consisted of close calls from the same subordinate group member as used in the test condition and in the second playback file, close calls from a different subordinate meerkat.

Playback protocol

Playback experiments were conducted on 8 male subordinate meerkats belonging to 8 different groups. All subjects were followed whilst foraging for a minimum of 30 minutes (range 0.5-2.5 hours) prior to playback. While the subject was foraging, both experimenters attached a loudspeaker (model: JBL on tour) to their legs at a height similar to that of another foraging meerkat and positioned themselves at geometrically opposite sides of

90 the subject. Experimenter one was approximately 2m from the subject to allow accurate filming of subjects at a
91 close distance, whilst experimenter two was approximately 5m from subject and 7m from experimenter 1 (Fig
92 1). The experimental setup was kept exactly the same in both test and control conditions so as to rule out any
93 distance-based effects due to asymmetrical speaker placement, that might otherwise explain subjects` response.
94 Keeping track of the spatial position of the two subordinates used as stimuli (to ensure spatial congruency), we
95 then played back from an iPod touch either different calls from the same individual from both sides (test
96 condition), or calls from two different individuals from both sides (control condition), with an approximately 4
97 second interval between stimuli. In the test condition, we therefore simulated an incongruent situation; that a
98 subordinate individual was relaxed and foraging on one side of the subject and then a few seconds later appears
99 on the opposite side 7m from its original position, again in a relaxed social foraging state. By presenting subjects
100 with different calls from the same individual, we ensure that any violation of expectation response in the
101 incongruent condition would be based on the listener's recognition that the calls came from the same individual,
102 not that they constituted the exact same stimulus. In the control condition, we simulated a congruent scenario:
103 the presence of two relaxed independently foraging meerkats on opposite sides of the subject. Subjects were
104 filmed by the observer closer to the subject for 30s prior to the beginning of the first playback and one minute
105 after the end of the second playback. To avoid order effects, we randomized the order in which subjects heard
106 test and control conditions.
107
108 *Behavioural responses*
109 We analysed videos frame-by-frame using iMovie (MAC OS, 2010). Because we were playing back close calls,
110 a frequently produced, low-arousal state vocalization, and because the situation we were simulating was not
111 socially significant in comparison to previous vocal individual recognition studies [11], we did not expect overt
112 behavioural responses to the violation-of-expectation setup. We therefore primarily focused on the employment
113 of vigilance behaviour, a common alert-related behaviour which meerkats are known to demonstrate during
114 socially or ecologically important events [10], for the duration of the second playback plus a 5 second time
115 window following the final call played back. This time window was specifically chosen to compensate for
116 possible responses to the final call played back and because all subjects had already returned to relaxed foraging
117 by this time. The first playbacks in both the test and control conditions were used to assess baseline vigilance
118 behaviour (see ESM). We noted: 1) each time the subject was observed to scan the surrounding terrestrial area;
119 2) the duration of each vigilance bout, defined as the frame at which the meerkat began vigilance after having

120 previously held its head in a different position to the frame at which the meerkat returned its head to a foraging
121 posture; and 3) if vigilance performed was in the direction of the speaker from which the second playback was
122 broadcast. To ensure accurate coding of videotapes a second observer blind-coded 50% of trials (8 videos, see
123 ESM).
124
125 *Statistical analysis*
126 Due to the non-normal nature of the data and the small sample size, we employed exact non-parametric tests [12,
127 see ESM].
128
129 **3. RESULTS**
130
131 Meerkats were more vigilant and vigilant for longer during the incongruent condition than the
132 congruent condition (vigilance frequency (mean +-SD): incongruent = 2.12 +-1.5, congruent
133 = 0.37 +-0.51, exact Wilcoxon test, Z=-2.38, p=0.016 (figure 2); vigilance duration (s):
134 incongruent = 2.17 +-2.21, congruent = 0.14 +-0.22, exact Wilcoxon test, Z=-2.41, p=0.016
135 (figure 2)). Subjects were also more likely to look towards the speaker during the incongruent
136 condition than the congruent condition (Number of looks at speaker: incongruent= 0.875 +-
137 0.64, congruent: 0, Exact sign test: p=0.031). Baseline vigilance behaviour did not differ
138 between conditions (vigilance frequency: incongruent = 0.12 +-0.35, congruent = 0.25 +-0.46,
139 exact Wilcoxon test, Z=-0.57, p=1.0) vigilance duration (s): incongruent = 0.25 +-0.7,
140 congruent = 0.53 +-1.03, exact Wilcoxon test, Z=-1.28, p=0.375).
141
142 **4. DISCUSSION**
143 Although vocal individual recognition is assumed to be widespread amongst non-primate
144 animals, clear experimental evidence obtained under natural settings is surprisingly elusive.
145 The lack of evidence is most likely due to the difficulty of empirically testing between
146 individual recognition and categorization based on social status [3]. Our results suggest that

147 when confronted with an impossible socio-physical scenario – the presence of the same
148 individual on two different sides - meerkats are more vigilant and more likely to look in the
149 direction of the expectancy violation, than when the presence of two different individuals is
150 simulated. In both conditions subordinates from within the same group were used as subjects
151 and playback stimuli; this allows us to rebut the common argument that discrimination occurs
152 only at the more rudimentary class or group level, leading us to conclude that meerkats
153 distinguish between individuals.
154
155 Meerkats live in stable, cooperatively breeding social groups of up to 50 individuals [13].
156 Individuals are continually exposed to a number of social challenges, including aggression,
157 competition for dominance and coordination of cooperative behaviours [14]. Keeping track of
158 conspecifics with whom individuals have differentiated competitive and cooperative relations
159 is therefore a crucial requirement for the successful maintenance of meerkat social systems.
160 Commonly emitted close calls, indicating the position and identity of the caller, may be one
161 medium through which this occurs.
162
163 A recent study at the same site has shown that subordinate female meerkats can recognize the
164 dominant female vocally [15]; however, given that there is only ever one dominant female in
165 each group, that study could not logically show this goes beyond category-level recognition
166 of dominant females. In the current study we have shown within-class discrimination of
167 subordinate individuals who are tracked spatially. Hence we suggest that meerkats do indeed
168 have a concept of conspecifics as “individuals” recognized perceptually. Exactly what
169 cognitive mechanisms underlie this discrimination is not clear. For example, this experiment
170 does not allow us to determine whether or not meerkats form a global representation of
171 individuals by integrating identity cues from multiple modalities [16]. The absence of

experimental evidence for multiple modality integration does not necessarily negate the presence of individual recognition through auditory cues alone. Humans recognize the voices of radio personalities they have never seen, and recent work in auditory perception suggests that short-term memory in hearing is based on auditory objects that bind related elements of the auditory scene into a single representation [17].

Understanding how animals experience the individuals within their social worlds is key to deciphering the evolution of social and communicative capacities as sophisticated as those in humans [18]. Our results, indicating individual recognition in a non-primate mammal under natural conditions, highlight the possibility that the task of monitoring the location of group members based on their vocalizations may employ recognition mechanisms similar to those demonstrated in more complex social interactions, such as third-party relationships, or coalition formations. We hope our results will encourage others to employ similar violation-of-expectancy experimental paradigms when natural social contexts in which to test individual recognition are lacking. This may ultimately allow more systematic cross-species comparison of individual recognition.

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Figures

Figure 1

Schematic design outlining the playback protocol used in both the incongruent (test) and congruent (control) conditions.

Figure 2

a) Frequency of vigilance and b) vigilance duration (mean+- 1SE) during both the incongruent (test) and congruent (control) experimental conditions.